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28. The chimeric receptors were expressed under the control of the apGal4 driver in the dorsal wing and notum. The chimeras that showed mild dominant-negative behavior did not affect wg expression at the dorsal/ventral (D/V) margin, indicating that the observed effect is due to Wg read-out defects in the third larval instar. Planar polarity was analyzed in the wing cell hairs (Fig. 3) and by the orientation of the microchaetae on the notum. Effects on planar polarity in the notum were seen with Fz1 and Fz2-1, as is the case in the eye and wing.
29. To analyze the effects of the chimeric receptors in the legs, we used DllGal4 as a driver (other Gal4 drivers resulted either in all chimeras having a wild-type appearance irrespective of the Fz receptors expressed or were lethal). DllGal4>Fz1 gave no detectable planar polarity phenotype, whereas DllGal4>Fz2 was lethal. Fz2-1 and Fz2-2-1 were pupal lethal, showing loss of distal leg structures, a dominant-negative Wg-related effect. Fz1-2 and Fz1-1-2 showed a mild Wg GOF phenotype, as judged by loss of the dorsally derived claws (indicating a transformation to ventral Wg-induced structures) [W. J. Brook and S. M. Cohen, Science 273, 1373 (1996)].
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32. A small difference in Fz signaling levels between the neighboring R3 and R4 cells is critical to establish correct ommatidial polarity and leads reproducibly to correct polarity; the small difference is amplified by Delta/Notch signaling [M. Fanto and M. Mlodzik, Nature 397, 523 (1999); M. T. Cooper and S. J. Bray, Nature 397, 526 (1999); A. Tomlinson and G. Struhl, Development 126, 5725 (1999)]. The rescue experiments demonstrate that the CRD of Fz1 and a putative ligand are important to establish this difference. Fz2-1 cannot respond to the ligand and establish this difference. Nevertheless, for constitutive activation of downstream pathways the Fz1 CRD is not required.
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39. We are grateful to P. Adler, K. Basler, S. Carroll, R. Carthew, S. Cohen, R. Nusse, and M. Strigini for fly strains and reagents. We thank members of the Bouwmeester and Mlodzik labs and M. Strigini and S. Cohen for discussions, and J. Curtiss for helpful comments on the manuscript. M.B. was supported by a predoctoral fellowship from the Boehringer Ingelheim Fonds, J.M. is a recipient of a long-term fellowship from the European Molecular Biology Organization.

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Economic Incentives for Rain Forest Conservation Across Scales

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Globally, tropical deforestation releases 20 to 30% of anthropogenic greenhouse gases. Conserving forests could reduce emissions, but the cost-effectiveness of this mechanism for mitigation depends on the associated opportunity costs. We estimated these costs from local, national, and global perspectives using a case study from Madagascar. Conservation generated significant benefits over logging and agriculture locally and globally. Nationally, however, financial benefits from industrial logging were larger than conservation benefits. Such differing economic signals across scales may exacerbate tropical deforestation. The Kyoto Protocol could potentially overcome this obstacle to conservation by creating markets for protection of tropical forests to mitigate climate change.

Each year, an estimated 13 million hectares of forests are destroyed (1), 5.6 to 8.6 Gt of carbon are emitted (2), and 14,000 to 40,000 species disappear from tropical forests (3). Greenhouse gas emissions are likely to increase Earth's temperature by 1° to 4°C in the next century, leading to the possibility of increasingly severe droughts and floods, enhanced rates of species invasion and extinction (4), and thus significant economic harm.

Tropical deforestation alone is responsible for 20 to 30% of carbon emissions (5) and most species extinction worldwide (6). Conserving tropical forests could therefore reduce both global warming and biodiversity loss (7). Despite conservation efforts, many "protected areas" in the tropics continue to be degraded, while unprotected forests are being converted by logging and agriculture (8). We analyzed the economic benefits of forest con-

servation from local, national, and global perspectives to determine the structure of incentives; ultimately, it is the interaction of these incentives across scales that will determine the fate of forests.

We used the Masoala National Park Integrated Conservation and Development Program (ICDP) in Madagascar as our case study, because it provided ample data for economic evaluation (9–13). The park (2300 km²) is composed of primary rain forest and is surrounded by a 1000-km² buffer of unprotected forest. Slash-and-burn farming for subsistence rice production represents the current principal threat to these forests. At current rates, farmers may reach the park boundaries in as few as 9 years. To counter

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deforestation, the Masoala ICDP's strategy is to create economic incentives for conservation, by working with local communities to develop markets for forest products from the buffer areas and nature-based tourism in the park (9).

Although local incentives are important, incentives at national and global scales are also essential to the success of conservation efforts, because national governments often make large-scale natural resource decisions affecting conservation, and the international community sponsors conservation through foreign aid and technical assistance. Conservation is most likely to succeed when benefits outweigh costs at the scales of all relevant decision-makers. To assess benefits and costs, we developed an opportunity-cost scenario and compared estimates of net benefits from the ICDP against the net benefits from the opportunity-cost scenario at local, national, and global scales. All estimates were calculated as net present values (NPVs) based on market values or shadow prices obtained with standard valuation techniques and appropriate local, national, and global data sources (see footnotes to Table 1). Two time-frames

(10 and 30 years, based on the length of a forestry concession in the opportunity-cost scenario) and three discount rates [3% (14), 10% (15), and 20% (16)] were used to test sensitivity. We report results as ranges (in U.S.$ 1996) over these time frames and discount rates. In some cases, ranges also include results from two other opportunity-cost scenarios (see below).

The opportunity-cost scenario is the land use that produces the highest alternative return. At the national level, the highest return would come from large-scale industrial forestry concessions. We assumed that such logging enterprises would be foreign-owned, bounded in scale based on the required capital investment, respect Malagasy laws, and invest the minimum in infrastructure to export high-value roundwood from Madagascar (17). It is unlikely, however, that Madagascar would receive all the financial benefits legally due from a large-scale logging operation (18). Thus, we also calculated a lower bound opportunity cost assuming that only a portion of the benefits (about 33%) would be captured by the nation (17). In both cases, we assumed that while logging "selectively,"

Table 1. Local, national, and global net benefits for the integrated conservation and development program [ICDP; see (17) for further details].

Discount rate	3%		10%		20%	
Time span of net present values	10 years	30 years	10 years	30 years	10 years	30 years
Local economy: impact of ICDP per community	U.S.$ 1996 × 10³					
Sustainable community forestry (9)	129.7	315.6	88.5	143.6	55.1	68.3
Ecotourism (17)	2.7	19.1	1.9	6.1	1.3	2.2
Nontimber forest products (NTFPs)*	86.6	221.6	61.9	101.0	41.9	51.0
Hill rice†	−11.5	−26.5	−8.3	−12.7	−5.7	−6.7
Opportunity cost: Large-scale forestry‡	−1.4	−3.2	−1.0	−1.5	−0.7	−0.8
Local net benefit	206.1	526.6	143.1	236.5	91.9	113.9
National economy: impact of ICDP	U.S.$ 1996 × 10⁶					
Donor investment§	7.81	9.95	6.01	6.80	4.43	4.66
Ecotourism/park employment (17)	7.06	42.49	5.10	12.91	3.50	5.16
Sustainable community forestry/biodiversity products (9, 13)	2.96	13.08	1.33	3.29	0.50	0.80
Sustained use of NTFPs*	7.28	28.57	4.71	11.01	2.77	4.27
Watershed protection value‖	0.58	3.40	0.38	1.13	0.22	0.38
Park/buffer zone management costs§	−8.97	−13.06	−6.70	−8.07	−4.79	−5.15
Internal benefit from ICDP project	16.73	84.44	10.83	27.07	6.64	10.12
Opportunity cost: Industrial logging concession‡	−92.57	−333.89	−56.36	−127.89	−30.02	−47.14
Opportunity cost: Hill rice farming†	−6.53	−15.00	−4.70	−7.22	−3.21	−3.81
Total opportunity costs	−99.10	−348.89	−61.06	−135.10	−33.23	−50.95
National net benefit	−82.38	−264.45	−50.23	−108.03	−26.59	−40.83
Global economy: impact of ICDP¶	U.S.$ 1996 × 10⁶					
Carbon conservation value @ $20/t C (27, 28)	188.94	655.41	122.35	260.66	71.97	105.11
Donor investment in ICDP	−7.81	−9.95	−6.01	−6.80	−4.43	−4.66
Global net benefit	181.13	645.46	116.34	253.85	67.54	100.45

*We calculated annual flows from NTFPs by cumulating the hectares of deforestation avoided each year, and multiplying by the annual value for sustained use of NTFPs [~$15/ha (9)]. NPVs were then calculated from these annual flows. †The value of one rice harvest after logging was estimated at $69/ha on the basis of typical rain-fed rice productivity on the Masoala Peninsula (13). ‡The national opportunity costs to Madagascar for not granting a large-scale logging concession included stumpage fees, taxes, employment, and infrastructure development. We based our model on similar timber companies operating in developing countries, assuming that expatriate investors (i) invest in minimum infrastructure, (ii) hire national staff primarily, (iii) harvest all currently exported hardwoods, (iv) export roundwood to mills outside of Madagascar, and (v) pay all taxes and fees legally due to Madagascar (full capture scenario). We used timber inventory data from Masoala (9, 13) to assess per hectare harvest levels, values and stumpage fees, and GIS to determine where harvesting was profitable (26). We assumed that half of the wood would be exported, and the rest sold domestically. At the local scale, opportunity costs equaled lost local employment from large-scale logging. See (17) for further details. §Donor investment and project costs were based on the current Masoala ICDP budget, assuming 5 years of aid for park management and 20 years for development, with diminished inputs after 10 years. ‖We calculated the annual value of watershed protection to irrigated rice agriculture and to marine fisheries by first obtaining a per hectare annual value for each watershed component, and then multiplying this value times the cumulative number of hectares deforested each year. For irrigated rice agriculture, we calibrated a watershed study from a nearby park (37). For fisheries (38), we divided the annual value of the artisanal marine fishery on Masoala (13) by the number of hectares of forest and multiplied by 0.5, because it is unlikely that forest clearing would reduce fisheries to zero. ¶To calculate global impacts of the ICDP, we estimated public values that are nonexcludable and nonrival benefits. We did not evaluate the net impact of forest conservation versus exploitation on private actors (e.g., logging, ecotourism, or international airline companies) or private goods (e.g., timber, souvenirs, or planes).

forests would be extensively damaged from road-building and mechanized harvest (*19*). Then, subsistence farmers would follow logging roads to slash-and-burn the high-graded forests (*18*); thus, the value of one rice harvest was calculated as part of the total opportunity cost. In 1995, however, Madagascar enacted environmental laws to prevent industrial-scale activities from degrading the environment (*20*). Consequently, we also developed and evaluated a "best management practices" scenario to compare with industrial logging (*21*).

To evaluate the ICDP scenario, we estimated projected financial costs and benefits from establishing and maintaining the Masoala National Park and its buffer zones. Benefits included employment, foreign aid, tourism, and the sustainable production of forest products, watershed protection, and carbon conservation resulting from prevention of projected deforestation. Costs included management of the park and implementation of development activities around the park. A major source of uncertainty in estimating these benefits was whether the ICDP would meet its stated goals, which include (i) arresting deforestation in the area, (ii) implementing community-based sustainable forestry projects in 50,000 ha over 15 years, and (iii) reaching ecotourism targets of 10,000 visitors per year within 5 years (*22*). Complex devel-

opment projects in developing countries have high failure rates (*15*). Our projections assumed that this ICDP will succeed; by comparison, the uncertainty resulting from data error is a minor problem.

At the local level, we found that communities would lose significant economic benefits if lands they were to use for community-based sustainable forest management and tourism were placed in large-scale logging concessions, whether sustainable or not. With the ICDP, communities would enjoy surpluses of $92,000 to $527,000 (*23*) over the industrial logging scenario (Table 1). A large proportion of this value is due to the subsistence use of nontimber forest products (NTFPs) for artisanal production, food, fuel, fiber, and construction (*10*, *11*), all key to quality of life for local residents.

While initially dependent on foreign aid in our model, we terminated aid to the Masoala park in year 5 and to the development component in year 20. Gross benefits to Madagascar from the ICDP, ignoring opportunity costs, ranged from $7 million to $84 million (Table 1) and were positive within 10 years. The ICDP would thus be a reasonable business proposition for Madagascar in comparison to current slash-and-burn land use on the peninsula.

The financial benefits from industrial logging concessions, however, exceeded the

ICDP's value (Table 1) even when the lowest estimates of revenue generated by logging were used. Although uncertainties exist in the estimate of opportunity cost, these three scenarios show that any large-scale logging operation would be significantly more profitable to the state than the ICDP, by $6 million to $265 million (Table 2).

Lucrative large-scale logging operations are leading to the destruction of many forests, particularly in Africa and Asia (*24*, *25*). We found no physical or economic barriers that would prevent large-scale logging companies from accessing the entire forest on the Masoala Peninsula (*26*). We estimated net annual returns on investment to large-scale logging companies and found profit margins of $2.37 million per year even for the least-profitable scenario, best management practices. Thus, large-scale logging is a realistic prospective land use for Masoala and similar areas.

Several timber companies were prospecting for concessions on the Masoala Peninsula during the time that the National Park was being established, and the government nearly abandoned the park project in favor of a logging company. The conservation and diplomatic community played a large role in persuading the government to reject the logging companies' proposals, using both political and economic arguments. Without this

Table 2. The cost of conserving carbon. Regardless of opportunity-cost scenario, when Madagascar conserves forests, it pays most of the costs of preventing transfers of carbon from the biosphere to the atmosphere.

Discount rate	Units	Full capture scenario for opportunity costs			Partial capture scenario for opportunity costs			Best management practices scenario for opportunity costs		
		3%	10%	20%	3%	10%	20%	3%	10%	20%
Timespan of NPV					10 years					
Net value of ICDP to Madagascar including logging	U.S.$ 1996 × 10⁶	−82.38	−50.23	−26.59	−21.29	−13.31	−7.18	−15.60	−10.14	−5.83
National opportunity cost of land	U.S.$ 1996/ha	−250	−152	−81	−65	−40	−22	−47	−31	−18
Madagascar's cost to conserve greenhouse gases	U.S.$ 1996/t CO_2 C	−3.91	−2.38	−1.26	−1.01	−0.63	−0.34	−2.47	−1.60	−0.92
Donor countries' cost to conserve greenhouse gases	U.S.$ 1996/t CO_2 C	−0.37	−0.29	−0.21	−0.37	−0.29	−0.21	−1.24	−0.95	−0.70
Total	U.S.$ 1996/t CO_2 C	−4.28	−2.67	−1.47	−1.38	−0.92	−0.55	−3.70	−2.55	−1.62
Proportion borne by Madagascar		0.91	0.89	0.86	0.73	0.69	0.62	0.67	0.63	0.57
Timespan of NPV					30 years					
Net value of ICDP to Madagascar including logging	U.S.$ 1996 × 10⁶	−264.45	−108.03	−40.83	−42.02	−23.29	−9.98	−19.81	−15.53	−7.60
National opportunity cost of land	U.S.$ 1996/ha	−801	−327	−124	−127	−71	−30	−60	−47	−23
Madagascar's cost to conserve greenhouse gases	U.S.$ 1996/t CO_2 C	−4.18	−1.71	−0.65	−0.66	−0.37	−0.16	−1.04	−0.82	−0.40
Donor countries' cost to conserve greenhouse gases	U.S.$ 1996/t CO_2 C	−0.16	−0.11	−0.07	−0.16	−0.11	−0.07	−0.52	−0.36	−0.25
Total	U.S.$ 1996/t CO_2 C	−4.34	−1.82	−0.72	−0.82	−0.48	−0.23	−1.57	−1.18	−0.65
Proportion borne by Madagascar		0.96	0.94	0.90	0.81	0.77	0.68	0.67	0.70	0.62

pressure, the Masoala Peninsula, one of Madagascar's most important reservoirs of biodiversity, would perhaps have become a forestry concession instead of a national park. However, many other countries do not have vigilant watchdog organizations and strict environmental laws (20), so logging often constitutes a serious threat to forests (24, 25).

The loss of Masoala's forests would be a significant economic cost to the international community ($68 million to $645 million) (Table 1). We estimated their global value on the basis of the damages avoided by preventing greenhouse gas emissions from the deforestation that would otherwise occur without the ICDP (17). To develop a conservative estimate, we used a damage cost of $20/t C (27), used an estimate of net committed emissions, and developed a schedule for the gradual release of greenhouse gases over a 10-year period (28). We did not include costs or benefits to private actors such as logging or ecotourism companies, because our concern at the global scale was with public goods and services. Nor did we include other significant global benefits, such as the option or existence value of biodiversity in Masoala's forests, because a market in these values is unlikely to emerge. These values would be high relative to other regions, however, because Madagascar is among the top five countries for plant and vertebrate endemism per unit area (29), with a globally unique and species-rich biota, and Masoala is one of its most significant biodiversity areas (9).

We then estimated the unit cost of conserving carbon [in metric tons of CO_2 C equivalents (28)] between $0.23 and $4.34 (Table 2); this range is comparable to per metric ton C costs for trial climate-related forestry and conservation projects (30). The unit cost can be partitioned into the global cost (foreign aid for forest protection) and Madagascar's cost (opportunities foregone). Madagascar, one of the world's poorest countries (31), is paying 57 to 96% of the total costs (Table 2), but itself would benefit relatively little from reducing global greenhouse gas emissions. While the Masoala ICDP was established to conserve biological diversity, not terrestrial carbon, the global community is reaping the concurrent public benefit of carbon conservation at the low cost of $0.07 to $1.24/t C.

Both Madagascar's opportunity costs ($18 to $801/ha) and the costs of conserving carbon vary by more than an order of magnitude, depending on the logging scenario, discount rate, and time-frame. Madagascar and many developing countries have high private rates of discount and poor ability to capture legal rents from forestry concessions (16, 18). Thus, the partial capture scenario with a discount rate between 10 and 20% is the most realistic estimate of the minimum market rate

required for compensation for carbon conservation (Table 2: 10-year NPV, $22 to $40/ha; 30-year NPV, $30 to $71/ha), corresponding to a cost of $0.16 to $0.63/t CO_2 C equivalents (32).

Estimates of damages from carbon release range from $5 to $100/t C, but probabilistic studies showed that $20/t C is a conservative estimate of mitigation of damages (27). Thus, by conserving carbon at <$1/t, one could generate a 20-fold surplus to pay transaction costs and buffer against the risk of individual project failure [e.g., one out of two development projects in Africa (15)]. Paying the opportunity cost for forest conservation is an economical mechanism for securing reduced greenhouse gas concentration (7), while promoting other benefits including the protection of a threatened biota of inestimable value (29), maintenance of ecosystem services, and promotion of human welfare. If Madagascar could receive the opportunity cost, it would then receive $10 million to $23 million (Table 2: 30-year NPV, partial capture scenario, discount rate 10 to 20%) for the value of the Masoala National Park and its surrounding buffer zone, instead of the $4.7 million to $6.8 million that we project it will receive (Table 1: 30-year NPV, donor investment, discount rate 10 to 20%). These funds would be sufficient to ensure the long-term protection of the park, whereas current budgets may be insufficient (22).

This case study suggests that the conservation and sustainable-use approach could provide significant economic benefits at all scales. At the national level, however, where decisions about conservation are generally made, large-scale logging currently provides better economic returns. We believe that similar split-incentive situations exist in many humid forested areas (24, 25) and other ecosystems (33) in the developing world.

The Kyoto Protocol, however, could secure net local, national, and global benefits equitably by recompensing nations for the opportunity costs of conservation through global transfers under the Clean Development Mechanism (34, 35), which would allow industrialized countries to exceed domestic emissions quotas by creating equivalent emissions reductions in a developing country (36). If such transfers do not occur, we can expect that many developing nations will continue to liquidate their forests for foreign exchange, although it is not in their best long-term interest (24, 25).

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15. World Bank, *1993 Evaluation Results: A World Bank Operations Evaluation Study* (World Bank, Washington, DC, 1993).
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17. Further descriptions of the industrial logging scenario, the other opportunity-cost models, and the ICDP valuation are available at *Science* Online at www.sciencemag.org/feature/ data/1047676.shl.
18. Like those in many developing countries, Madagascar's forestry department lacks the resources to police large-scale operations or capture all rents to which it is entitled. See also The Asia Pacific Action Group, "The Barnett Report" (The Asia Pacific Action Group, Hobart, Tasmania, Australia, 1990); E. Barbier, J. Burgess, J. Bishop, B. Aylward, in *The Causes of Tropical Deforestation*, K. Brown and D. W. Pierce, Eds. (Univ. of British Columbia Press, Vancouver, Canada, 1994), pp. 271–295.
19. A. G. Johns, *Timber Production and Biodiversity Conservation in Tropical Rain Forests* (Cambridge Univ. Press, Cambridge, 1997).
20. Mise en Compatibilité des Investissements avec l'Environnement (MECIE), Decret No. 95-377. The International Tropical Timber Organization also has a goal of achieving trade in sustainably managed timber by 2000 [Asia Pacific Forestry Sector, "Asia-Pacific Forestry towards 2000" (Food and Agricultural Organization, Rome and Bangkok, 1998)].
21. The best management practices scenario would cut 1 m³/ha per year [I. A. Bowles, R. E. Rice, R. A. Mittermeier, G. A. B. da Fonseca, *Science* **280**, 1899 (1998)] to manage the forest sustainably on a 60-year rotation, reducing productivity/hectare to 40%. Forbidding logging on high slopes and within 100 m of streams would reduce the logging area by 44%, but improved efficiency from planned logging operations (~22%) would offset the area reduction [see P. Barreto et al. in (16)]. We assumed that the concession-

aires would succeed in preventing slash-and-burn farming in 70% of the concession. For further details, see (17).

22. M. C. Hatchwell, personal communication.
23. Figures are rounded in the text to avoid false precision.
24. D. M. Wolfire, J. Brunner, N. Sizer, Forests and the Democratic Republic of Congo (World Resources Institute, Washington, DC, 1998).
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26. We used Geographic Information System (GIS) to determine if road-building costs or transport costs limit access to particular areas. A cost-surface, calculated as the total distance to the nearest existing road or port multiplied by the cost per kilometer of building new roads and transporting timber, was consistently offset by the financial benefits of harvesting the timber up to 50 km; thus, no constraints operated within an area the size of the Masoala Peninsula ($\sim$4000 km^2). See also (17).
27. S. Fankhauser, Valuing Climate Change: The Economics of the Greenhouse (Earthscan, London, 1995). For the year 1995, 50% of simulation runs estimated an optimal carbon tax >$20/t C, and optimal tax levels associated with a given probability increased each year [T. Roughgarden and S. H. Schneider, Energy Policy 27, 415 (1999)].
28. Net committed emissions take into account the total weighted emissions of greenhouse gases over time from deforestation and the uptake of gases due to regrowth, and are calculated in CO_2 C equivalents that account for varying greenhouse gas potentials and ratios of different gases. We assumed that burning a hectare of primary rain forest, with reburns every $\sim$3 years, would result in the net release of $\sim$191 metric tons of CO_2 C equivalents [P. M. Fearnside, Climatic Change 35, 321 (1997)]. We further assumed that release of carbon would be amortized over 10 years. Due to the time value of money, this timed release reduced the NPVs of greenhouse gas conservation by $\sim$1.8 times.
29. R. Mittermeier, N. Myers, J. Thomsen, Conserv. Biol. 12, 516 (1998).
30. R. Schwarze [Ecol. Econ. 32, 255 (2000)] found an average cost per ton of CO_2 of $2.6 for land use, cover change, and forestry projects; see S. Brown et al. in (5).
31. Population Reference Bureau, "World Population Data Sheet 1995" (Population Reference Bureau, Washington, DC, 1997).
32. Although the best management practices scenario generates similar opportunity costs, it would be more difficult for Madagascar to implement than simple protection of the forest [see I. A. Bowles et al. in (21)], and therefore less likely to prevent deforestation reliably and to obtain carbon credits (36); nor would it provide the biodiversity benefits of strict conservation [J. Robinson, Conserv. Biol. 7, 20 (1993)].
33. For example, semi-arid savannahs [B. Walker, Envir. Dev. Forum 4, 204 (1999); see also references in (18)].
34. J. O. Niles and R. Schwarze, in Proceedings of the IEA Bioenergy Task25 Workshop: Bioenergy for Mitigation of CO_2 Emissions: The Power, Transportation and Industrial Sectors, K. Robertson and B. Schlamadinger, Eds. (International Energy Agency, Graz, Austria, 2000).
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36. Preventing deforestation is an emission reduction, whereas planting trees is a sequestration process. Currently, conserving forests has stronger legal status under the Clean Development Mechanism because it is an emission reduction. The Kyoto Protocol requires verification of real, measurable, voluntary, and long-term reductions. Costa Rica has evolved strategies for dealing with leakage and additionality [D. C. Goldberg, R. Castro, S. Mack, "Carbon conservation: Climate change, forests and the Clean Development Mechanism" (Center for International Law, Centro de Derecho Ambiental y de los Recursos Naturales, Washington, DC, 1998)]. Ultimately, however, industrialized countries will also have to reduce their own

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mGluR1 in Cerebellar Purkinje Cells Essential for Long-Term Depression, Synapse Elimination, and Motor Coordination

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Targeted deletion of metabotropic glutamate receptor–subtype 1 (mGluR1) gene can cause defects in development and function in the cerebellum. We introduced the mGluR1α transgene into mGluR1-null mutant [mGluR1 (–/–)] mice with a Purkinje cell (PC)–specific promoter. mGluR1-rescue mice showed normal cerebellar long-term depression and regression of multiple climbing fiber innervation, events significantly impaired in mGluR1 (–/–) mice. The impaired motor coordination was rescued by this transgene, in a dose-dependent manner. We propose that mGluR1 in PCs is a key molecule for normal synapse formation, synaptic plasticity, and motor control in the cerebellum.

mGluRs are G protein–coupled glutamate receptors and are implicated in modulation of synaptic transmission and plasticity (1). mGluR1 (–/–) mice have characteristic cerebellar symptoms such as ataxic gait, intention tremor, and motor discoordination (2–4). The blockade of mGluR1 by antiserum to mGluR1 results in ataxia, suggesting that mGluR1 is required for motor coordination (5). In mGluR1 (–/–) mice, the anatomy of the cerebellum, the morphology of PCs, and the synaptogenesis onto PCs from parallel fibers (PFs) are normal. However, developmental transition from multiple to mono-innervation of PCs by climbing fibers (CFs)

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(6), the other excitatory input to PCs (7), is impaired during the third postnatal week (8). Long-term depression (LTD) at PF-PC synapses is clearly deficient in mGluR1 (–/–) mice (3, 4). Thus, mGluR1 is thought to be essential for CF synapse elimination and LTD induction, and its disruption may contribute to motor deficits of mGluR1 (–/–) mice. However, mGluR1 is expressed in various cell types in the central nervous system (CNS) other than PCs. Hence it is not clear to what extent mGluR1 in PCs contributes to these phenotypes.

We introduced a transgene (L7-mGluR1) that expressed mGluR1α under the control of the PC-specific L7 promoter (Fig. 1, A and B) into the mGluR1 (–/–) mice. One line of transgenic mice homozygous mutant for endogenous mGluR1 allele showed the cerebellum-restricted expression of the transgene (Fig. 1C) (9). (We refer to these mice as mGluR1-rescue mice.) The amount of mGluR1α protein in mGluR1-rescue cerebella was about 80-fold less than that in wild-type cerebella (Fig. 1C). mGluR1α immunoreactivity was abundant in the cerebellum, olfactory bulb, and thalamus in wild-type mice, whereas it was restricted to the